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# Stand tall and they still get you in your Achilles foot-pad

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The free-living first-instar larvae of Strepsiptera (Insecta) are the infective stage of the parasitoid. They normally enter the host via the abdominal cuticle, and there have also been reports of entry via the egg of the host. The first-instar larvae of *Stichotrema dallatorreanum* Hofeneder in Papua New Guinea were found to enter the host orthopteran via the tarsi. This is, to my knowledge, the first report of entry of first-instar larvae of Strepsiptera via the attachment pads (euplantulae) of the host.

**Keywords:** Strepsiptera; Orthoptera; Tettigoniidae; euplantulae

## 1. INTRODUCTION

Some insects have two distinct larval stages with different functions: in the first stage they locate the host, and the second stage is spent endoparasitically in the host. The host-seeking stage is always the active stage, spent in the open environment; on entry into the host, the larva moults to a feeding stage. Examples of two distinct larval stages (hypermetamorphosis) are found in Neuroptera (Mantispidae), Coleoptera (Meloidae, Rhipiphoridae, Staphylinidae), Diptera (Acroceridae, Bombyliidae, Nemestrinidae, Calliphoridae, Tachinidae), Hymenoptera (Perilampidae, Eucharitidae, Ichneumonidae: *Euceros*) and Strepsiptera (all families).

The first-instar free-living host-seeking stage of Strepsiptera normally enters and infects host nymphs or larvae via the abdomen (Lindberg 1939; J. Kathirithamby, personal observation). However, Kirkpatrick (1937) observed that the first-instar larvae of *Corioxenos antestiae* Blair (Corioxenidae) entered almost any part of the heteropteran host *Antestia* spp., and that the first-instar larvae of *Eoxenos laboulbenei* De Peyerimhoff (Mengenillidae) entered the thysanuran host *Lepisma* spp. via the coxa (Pohl 1998). Strepsipteran first-instar larvae have also been reported to enter the eggs of hymenopteran hosts (Linsley & MacSwain 1957; Krombein 1967; Maeta *et al*. 2001).

In Strepsitera the male endoparasitic larva emerges as a free-living adult after pupation in a living host; the female larva remains endoparasitic (except in one family) and becomes a neotenic adult. The endoparasitic neotenic females produce viviparous free-living first-instar larvae, which emerge to seek new hosts. The dispersion of the first-instar larvae is carried out by the stylopized living hosts, which remain mobile in spite of harbouring a female strepsipteran. Normally, the host dies only after the emergence of all the free-living first-instar larvae from the endoparasitic mother (Kathirithamby 1989), but recently it was observed that the first-instar larvae of *Xenos vesparum* Rossi continued to emerge even after the hymenopteran host *Polistes dominulus* Christ had died (J. Kathirithamby and L. Beani, personal observation). This phenomenon must occur only on rare occasions.

## 2. METHODS

### (a) *Insects studied*

The species studied was *Stichotrema dallatorreanum* Hofeneder, parasitic in *Segestidea novaeguineae* (Brancsik) (Tettigoniidae) and *Segestidea defoliaria defoliaria* (Uvarov), both serious pests of oil palm in Papua New Guinea (Kathirithamby *et al*. 1998), from Oro Province and West New Britain Province.

### (b) *Microscopic techniques: 5 μm sections*

The specimens were placed in 70% alcohol, passed through a graded series of alcohols for *ca*. 1 h each, placed in Histoclear for 1 h with two changes, then in hot wax at 57 °C for 30 min with two changes, and embedded in Polywax. An American Optical 820 Rotary Microtome (Leica, Germany), was used to cut 5 μm sections, which were mounted on 1% gelatinized slides with 1% glycerine albumen, blotted with wet fibre-free paper, dried on a hot plate, stained with Masson trichrome and observed under a Leica MPS 30 compound microscope (Leica Mikroskopie und System GmbH, Wetzlar, Germany).

The photographed whole specimens had been preserved in 75% alcohol in the field. They were photographed with a Zeiss stereomicroscope SR (Carl Zeiss Ltd, Oberkochen, Germany).

### (c) *Numbers studied*

I examined and studied 50 specimens of *S. novaeguineae* and 50 of *S. defoliaria defoliaria*, together with 20 5 μm sections of each species.

## 3. RESULTS AND DISCUSSION

Here, I report first-instar larvae of the strepsipteran *S. dallatorreanum* (Myrmecolacidae), which enter and infect the host Tettigoniidae, *S. novaeguineae* and *S. defoliaria defoliaria* (Orthoptera), in Papua New Guinea, not only via the abdomen of the host but also via the attachment pads (euplantulae) on the host's legs (figure 1). In the 100 specimens examined, first-instar larvae were present in the tarsi, and apodous second-instar larvae (which had moulted from the first-instar larvae) were present in the tibia (figure 1*b*), femur and thorax of the hosts. Upon entry into the attachment pads, the first-instar larvae moult to endoparasitic apodous second-instar larvae, which then move up the leg, via the tarsi, tibia and femur, to the


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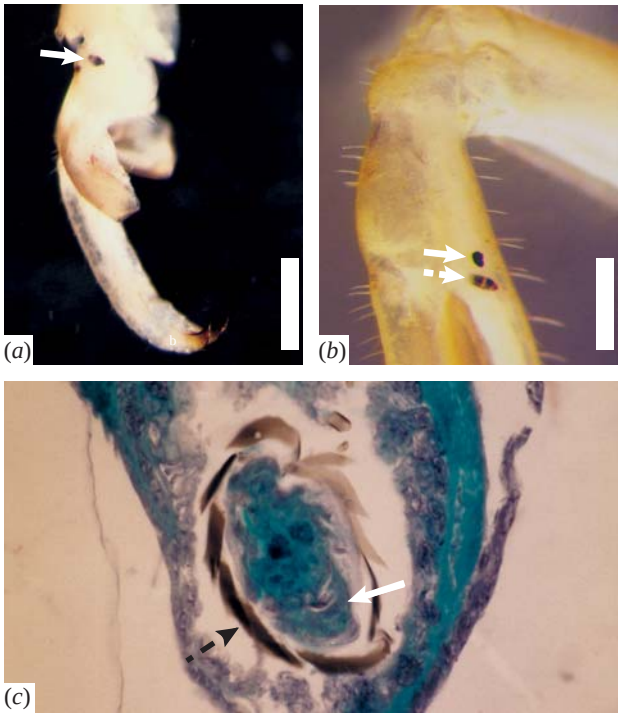


Figure 1. (*a*) Euplantulae of *Segestidea defoliaria defoliaria* (Uvarov) with endoparasitic first-instar larva of *Stichotrema dallatorreanum* Hofeneder (white arrow). (*b*) Tibia of *S. defoliaria defoliaria* with moulting first-instar larva of *S. dallatorreanum* (white arrow indicates the head of the first-instar larva; dashed white arrow indicates the thorax and abdomen of the first-instar larva). Scale bars in (*a*) and (*b*) represent 0.4 mm. (*c*) A 5 µm section of euplantula with an endoparasitic first-instar larva of *S. dallatorreanum* (dashed black arrow) and a pharate apodous second-instar larva (white arrow) within the first-instar larva; ×86.

thorax and, eventually, to the abdomen, where they complete their larval development. The shed cuticle of the first-instar larva is dragged along with the second and subsequent instars (figure 1*b*). *S. dallatorreanum* is a parthenogenetic species (J. Kathirithamby, unpublished data) and develops in an orthopteran host (Kathirithamby *et al.* 1998).

The unique structure of the attachment pads (euplantulae) of the bush cricket, *Tettigonia viridissima* (Orthoptera: Tettigoniidae), was described by Gorb & Scherge (2000). As in all other Tettigoniidae, there are four euplantulae in each tarsus, the terminal one being the largest. The inner and outer architectures of the pads provide stability and flexibility, which help the insect to walk upside down on vertical surfaces, prevent sliding, and also enable it to adapt to substrate roughness, which mobile insects such as Tettigoniidae are likely to encounter.

Tettigoniidae are large, and their abdominal surface is held above the surface of the palm fronds; the most convenient point of contact on the host for the free-living first-instar larvae (dispersed on the palm fronds as they emerge from the endoparasitic mother) is the attachment pads of the tettigoniid. Moreover, Tettigoniidae move fast, and the palm fronds are often wet from tropical rain. In the attachment pads the exocuticle is absent (Gorb & Scherge 2000). This would enable the first-instar larva to enter the host tettigoniid more quickly at this point than at any other point on the body. In other strepsipteran species the first-instar larvae enter the host fairly swiftly (within 30 min) when they come into contact with the host's cuticle. The attachment pads of Tettigoniidae are, therefore, the most convenient and speedy point of entry for a waiting first-instar larva of *S. dallatorreanum*.

## 4. CONCLUSION

This is, to my knowledge, the first report of the entry of an entomophagous parasite via the tarsi of a host, and of first-instar larvae of Strepsiptera infecting a host via the euplantulae. As far as I am aware, there are only five records of female Strepsiptera parasitic in Orthoptera (Kathirithamby 1998; Kathirithamby *et al.* 2001). The extremely unusual dual host–parasite relationship of the sexes of the Myrmecolacidae, where the females parasitize Orthoptera and the males parasitize Hymenoptera (Formicidae) (Kathirithamby & Hamilton 1992), has rarely been recorded. This might be due to the fact that the attachment pads (euplantulae) and legs of Orthoptera have not been checked for stylopization. When looking for strepsipteran parasitism of Tettigoniidae, therefore, it is advisable to examine not only their abdomens but also their attachment pads. The dark cuticle of the first-instar strepsipteran larva is clearly visible through the light cuticle of the host tettigoniid (figure 1*a*,*b*).

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